A TINY MICROSAUR FROM THE LOWER PERMIAN OF TEXAS: SIZE CONSTRAINTS IN PALAEOZOIC TETRAPODS

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ABSTRACT. *Quasicaecilia texana* gen. et sp. nov., from the Lower Permian of Texas, is a very small microsaur in which the nasal bones form the front margin of the skull and the cultriform process of the parasphenoid is not in contact with the sphenethmoid. The bones of the otic-occipital region are fused to one another, and the otic capsule and stapes are very large relative to other cranial dimensions, giving a superficial resemblance to modern caecilians. Many of the unusual cranial features of this species may be attributed to its small size. The relatively large size of the sensory capsules in Palaeozoic amphibians with an adult skull length less than about 2 cm results in significant modification of the area of the otic capsule and jaw articulation.

PALAEOZOIC amphibians have customarily been divided into two large groups, the labyrinthodonts and the lepospondyls (Romer 1966; Carroll 1977, 1987). Labyrinthodonts are typified by a suite of primitive characters inherited from their ancestors among the rhipidistian fish.

a. Squamosal embayment of cheek occupying position of rhipidistian operculum.
b. Marginal teeth exhibiting labyrinthine enfolding.
c. Large palatal fangs and associated replacement pits.
d. Occipital condyle (where present) narrow and circular.
e. Multipartite atlas-axis complex.
f. Vertebral centra primitively consisting of crescentic ventral intercentrum and paired pleurocentra.

Lepospondyls are characterized by a suite of more derived characteristics.

a. Absence of squamosal embayment.
b. Lack of labyrinthine enfolding of marginal teeth.
c. Absence of large palatal fangs and adjacent replacement pits.

Most lepospondyls have a wide or double occipital condyle and a single cylindrical centrum per segment.

Labyrinthodonts are certainly a paraphyletic group, including the ancestors of all more-derived tetrapods. Several recent attempts have been made to establish the affinities of the many groups termed lepospondyls, but as yet no consensus has been reached as to their specific relationships to the labyrinthodont groups, or to one another (Thomson and Bossy 1970; Gaffney 1979; Gardiner 1983; A. R. Milner *et al.* 1986; Gauthier *et al.* 1988; Panchen and Smithson 1988). In the absence of generally accepted relationships, it remains convenient to retain the descriptive terms labyrinthodont and lepospondyl.

In addition to similar derived features by which all lepospondyls are distinguished from labyrinthodonts, each individual group – aistopods, nectrideans, adelogyrinids, lysorophids and microsaurs – is distinguished from the others by numerous unique derived features. Lepospondyls also show a much higher degree of variability within each order than that exhibited by the labyrinthodonts in the pattern of the dermal bones of the skull, the configuration of the braincase, the length of the vertebral column, and the proportions and structure of the limbs. Labyrinthodonts

had a basically similar skeletal pattern from their first appearance in the fossil record in the Upper Devonian to their last appearance in the Cretaceous.

Shared derived features of the skeleton demonstrate that all tetrapods share a common ancestry above the level of the rhipidistian fish (Panchen and Smithson 1987). This implies that lepospondyls must have evolved from tetrapods having an anatomical pattern similar to that of known labyrinthodonts; however, no intermediates are recognized. This situation suggests that some complex of evolutionary constraints acted to retain a stereotyped anatomical pattern among the labyrinthodonts. The emergence of the various lepospondyl groups may be attributed to circumvention of these constraints.

In addition to the anatomical differences already mentioned, all lepospondyls are further distinguished from primitive labyrinthodonts by their smaller adult size. Some labyrinthodonts are as small as large lepospondyls, indicating that small size is not a *sufficient* factor in itself to result in the evolution of lepospondyl characters, but it seems a *necessary* factor, since none of the lepospondyls is the size of large labyrinthodonts. The larger Permian lepospondyls are highly derived members of this assemblage; all the early lepospondyls are much smaller.

Small size is an important attribute of the origin of many vertebrate groups: the modern amphibian orders (Carroll and Holmes 1980; Milner 1988), amniotes (Carroll 1970), and some lizard families (Rieppel 1988). Hanken (1983, 1989) has stressed its importance in the radical reorganization of the limbs and skulls of tiny living salamanders. The peculiar anatomy of the animal described in this paper provides a basis for considering the importance of skull size in influencing the cranial anatomy of Palaeozoic amphibians.

MATERIALS AND METHODS

This paper deals primarily with a single specimen (Text-fig. 1) collected by C. H. Sternberg in 1917 from the classic Texas Permian redbeds. The specimen had long been identified as *Cardiocephalus*, a gymnarthid microsaur. The short antorbital region may have been attributed to breakage, and the great width of the parietals may not have been recognized due to the presence of longitudinal cracks that might have been identified as sutures separating relatively narrow parietals from more lateral tabular bones.

As preserved, the skull is approximately 14·5 mm long, and equally as wide. The anterior extremity is formed by the broad, short nasal bones. They show no area for attachment of the premaxillae, and those bones are otherwise missing. The posterior surface of each occipital condyle is broken off, precluding exact determination of the length of the skull. Most of the bones of the palate are missing or displaced, exposing the braincase ventrally.

The skull roof and occiput were largely exposed as a result of natural weathering of the matrix. The parasphenoid was also initially exposed. The remaining areas of the palate and braincase were prepared with a fine needle. The matrix is a hard, fairly homogeneous limey clay. It varies in colour from white to pink and in places was very difficult to differentiate from the bone.

SYSTEMATIC PALAEONTOLOGY

Class AMPHIBIA Linnaeus, 1758
Order MICROSAURIA Dawson, 1863
Suborder MICROBRACHOMORPHA Carroll and Gaskill, 1978
?Family BRACHYSTELECHIDAE Carroll and Gaskill, 1978
Genus QUASICAECILIA gen. nov.

Type species. Quasicaecilia texana sp. nov.

Derivation of generic name. The generic name refers to several similarities with modern caecilians that are almost certainly not indicative of close relationship.
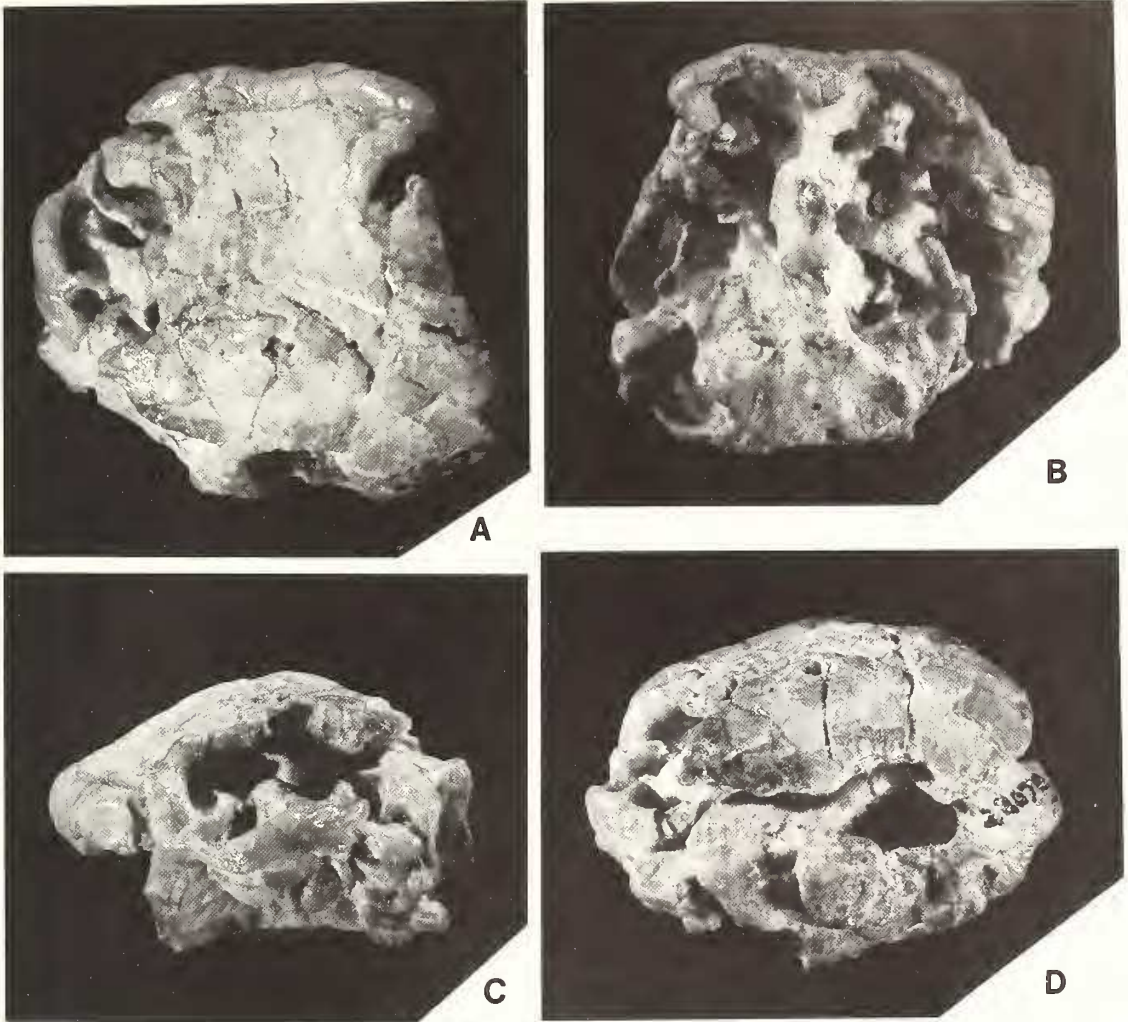
TEXT-FIG. 1. *Quasicaecilia texana*, type, United States National Museum, 22079. A, dorsal view of skull. B, obliquely anterior view of palate and braincase; postorbital bone that appears in drawings was removed prior to photographing. C, left lateral view of skull. D, occipital view of skull. All ×4.

Diagnosis. Microbrachomorph microsaur, possibly belonging to the family Brachystelechidae, differing from *Brachystelechus* and *Carrolla* in having extremely short and broad nasals that show no area of articulation for the premaxillae. Stapes apparently lacking stapedial foramen. Cultriform process of parasphenoid separated from sphenethmoid by wide gap.

Quasicaecilia texana sp. nov.

Text-figs 1–5

Derivation of trivial name. Refers to the state from which the type species was collected.

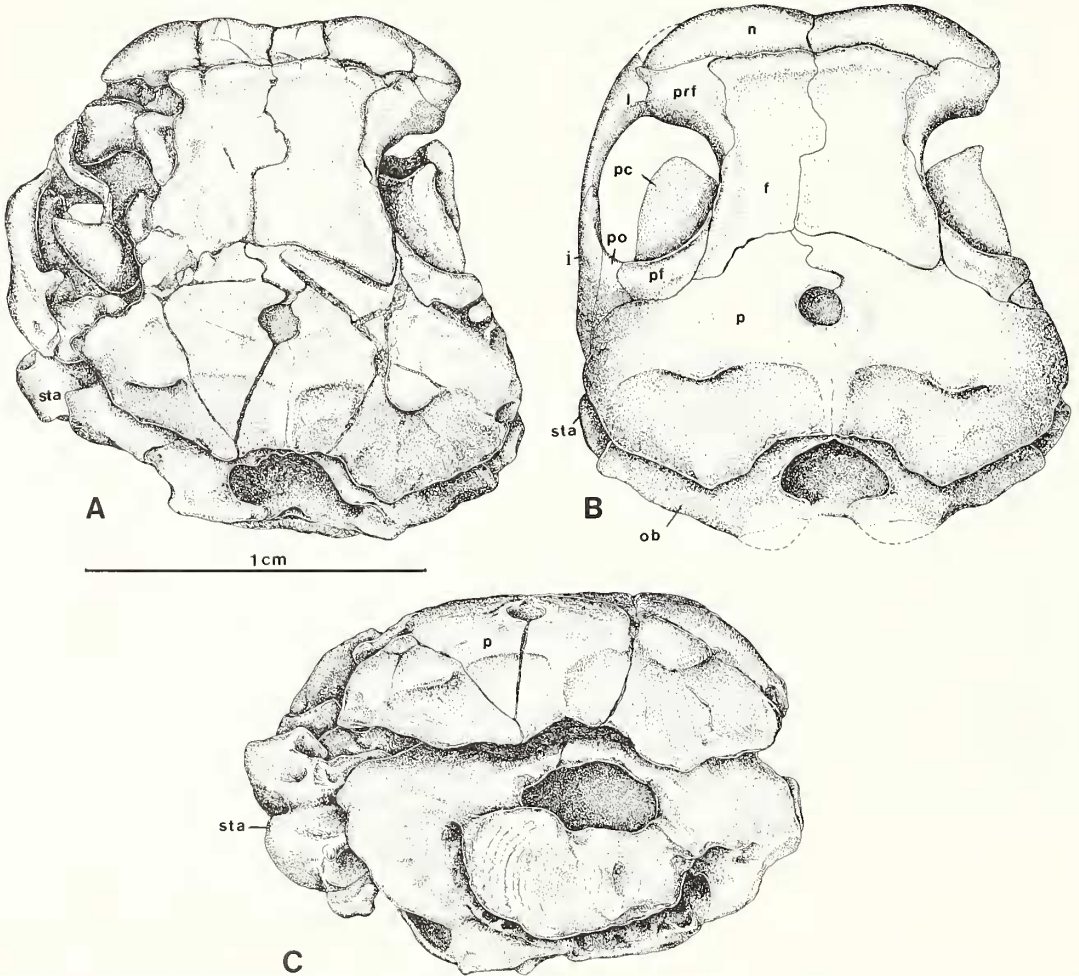*Holotype.* United States National Museum (USNM) no. 22079.

Locality and horizon. ?Baylor County, Texas; Lower Permian ?Arroyo Formation.

Diagnosis. As for genus. This is the only recognized species.

Description. Both the orbital and pineal openings appear large relative to the length of the skull, as would be expected in a small animal. The orbits are protected by large saucershaped palpebral bones. The surface of the roofing bones is essentially smooth and shows no evidence of lateral line canals.

The pattern of the skull roof (Text-fig. 2) differs dramatically from that of all other Palaeozoic tetrapods.


TEXT-FIG. 2. *Quasicaecilia texana*, type, United States National Museum, 22079. A, dorsal view of skull. B, reconstruction of skull in dorsal view. C, occipital view. All ×4·5. Abbreviations: a, angular; ba, basicranial articulation; bo, basioccipital; bs, basisphenoid; c, coronoid; cg, groove for carotid artery; com, composite of posterior jaw bones; d, dentary; dp, dorsal process of stapes; ect, ectopterygoid; eo, exoccipital; f, frontal; f-p, frontoparietal; j, jugal; l, lacrimal; m, maxilla; n, nasal; ob, os basale; opis, ophisthotic; otic, position of otic capsule; p, parietal; pal, palatine; pc, palpebral cup; pca, palatine canal; pf, postfrontal; pl, pleurosphenoid; pm, premaxilla; po, postorbital; pp, postparietal; prf, prefrontal; pro, prootic; ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; sa, surangular; sm, septomaxilla; so, supraoccipital; sp, splenial; sph, sphenethmoid; sq, squamosal; st, supratemporal; sta, stapes; syt, synotic tectum; t, tabular; t-sq, bone occupying position of tabular and squamosal; v, vomer; X, area of matrix left for support of cultriform process of stapes; ?, bone of uncertain identity; I, II, V, foramina for cranial nerves.

It consists primarily of very wide parietal bones, rectangular frontals, and wide and extremely short nasals. The nasals are rounded anteriorly to form the anterior margin of the skull. They extend ventrally so as to surround the area that would have been occupied by the nasal capsules. No bone occupies the position expected of the premaxillae at the anterior margin of the skull roof or palate. Since there is no area for their articulation with the nasals, it is probable that they were not solidly attached to the skull. There is no trace of postparietal bones. The parietals, as in modern caecilians, extend far posteriorly over the back of the braincase. Behind the pineal opening they appear fused at the midline where the bone forms a ridge that extends nearly to the margin of the foramen magnum between two areas that are recessed to receive the epaxial musculature. A transverse ridge on the patietals clearly demarcates the anterior limit of this musculature. On each side, the ridge is bowed posteriorly and slightly overlaps the occipital surface. There is no evidence of the large tabular bones that characterize tuditanomorph microsaurs.

The frontal narrowly enters the orbital margin between the pre- and postfrontals. All three bones form a wide medial margin to the orbit. The left postfrontal is missing, revealing a thick area of the parietal to which it was attached. On the right side, a small triangular remnant of the postorbital is retained in place between the postfrontal and the parietal. The remainder of the bone is broken off and appears in palatal view, with the lateral surface exposed medially. The entire bone is triangular in outline. The left jugal appears in more or less its natural position beneath the orbit. The remainder of the cheek region (Text-fig. 5) is badly crushed, making determination of its original configuration extremely difficult. The great size of the otic capsule indicates that the jaw articulation must have been far anterior in position. This is confirmed by the presence of the quadrate just behind the orbital opening. Presumably the squamosal occupied a narrow vertical area behind the jugal and wrapped around the quadrate posteriorly. The broken nature of the bone surface behind the jugal precludes determination of the presence or absence of the quadratojugal. The quadrate is the shape of a thickened vertical plate. The dorsal end is angled towards the posterior margin of the orbit. The lateral portion of the lower end forms a hemispherical condyle. More medially, the distal surface is broadly embayed for a distance that is as great as the width of the condyle. The medial edge is in contact with the quadrate ramus of the pterygoid. The shortness of the cheek and the large size and orientation of the quadrate indicate that the adductor chamber must have been very small, providing little space for jaw-closing musculature.

A thin crescent of bone above the distal end of the jugal may be the left palpebral cup. Beneath this is an area of bone that may be the lacrimal, although no opening for a lacrimal duct is evident. No trace of the maxillae can be identified.

A large triangular bone on the left side of the palatal area (Text-fig. 3) is identified as the pterygoid. Its
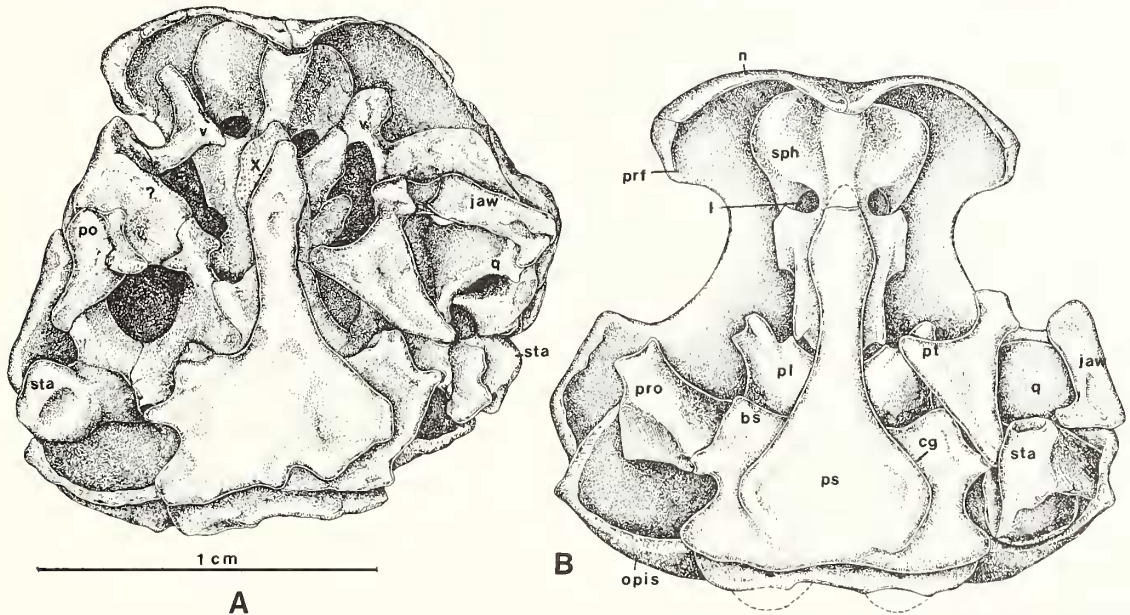
TEXT-FIG. 3. *Quasicaecilia texana.* A, palatal view of skull. B, reconstruction of palate; right side shows braincase with elements of palate and stapes omitted. ×4·5.

posterior end is in contact with the medial surface of the quadrate. Medially, it may have been in contact with a small unfinished surface of the prootie. The posteromedial surface of the bone shows no evidence of the basicranial articulation. Laterally, the bone angles sharply dorsally. A similar dorsal projection was noted in *Carrolla* by Langston and Olson (1986). The anterior surface of the bone is broadly concave. This implies an unusual outline for the interpterygoid vacuities, but this area might have accommodated retraction of the relatively large eyes. Anterolaterally, the pterygoid ends in an enlarged surface that appears to terminate in an oval area of articulation. This might have attached to the ectopterygoid or palatine.

Bone is visible on the right side between the orbit and the base of the braincase, but none of the surfaces is sufficiently well preserved to permit identification. Anteriorly, on both sides, are smaller bones with two rami meeting at nearly right angles. They are logically identified as the vomers. They lie adjacent to the sphenethmoid; presumably they were displaced from a more ventral position.

Above the scattered and difficult to identify palatal elements is a heavily ossified braincase (Text-figs 4 and 5). Its degree of ossification is matched by that of aistopods, but its structure is unique among Palaeozoic tetrapods. The braincase consists of two major elements, the anterior sphenethmoid, broadly comparable to the sphenethmoid of Palaeozoic labyrinthodonts, and the posterior otic-occipital complex. The latter incorporates all the bones recognized in other Palaeozoic tetrapods, fused into an essentially unipartite structure. The basioccipital, exoccipitals, supraoccipital, basisphenoid, laterosphenoids (or pleurosphenoids), opisthotics, prooties and parasphenoid are all fused without trace of sutures, except possibly the dorsal contact between the opisthotie and prootie. The resulting structure vaguely resembles the os basale of caecilians.

The articulating surface of the basioccipital and exoccipitals is lost, but would have been very wide as in typical microsaurs. The ventrolateral surface of these bones is deeply grooved just above the area of the parasphenoid. This groove is irregularly pitted, probably for insertion of hypaxial musculature to lower the head. Nerves X–XII presumably exited in this area, but their foramina cannot be differentiated with certainty from the other pits.

One of the most striking features of this tiny skull is the relatively enormous size of the otic capsules and stapes. The otic capsules extend to the lateral extremities of the skull as preserved. The fenestrae ovales appear huge in ventral view. They are almost 4 mm in dorsoventral extent. Their configuration differs somewhat on the two sides. On the right side the opisthotic rim extends further laterally than the prootie. On the left side
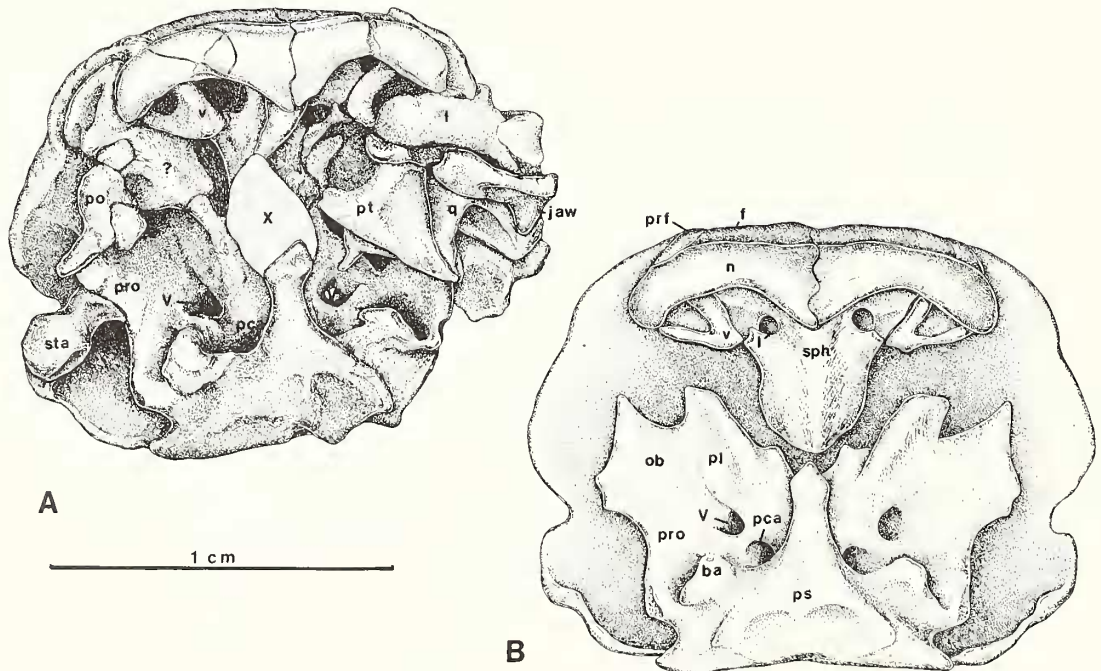
TEXT-FIG. 4. *Quasicaecilia texana.* A, oblique anteroventral view of skull. B, reconstruction of skull in anteroventral view. Most palatal elements have been omitted to expose braincase. × 4·5.
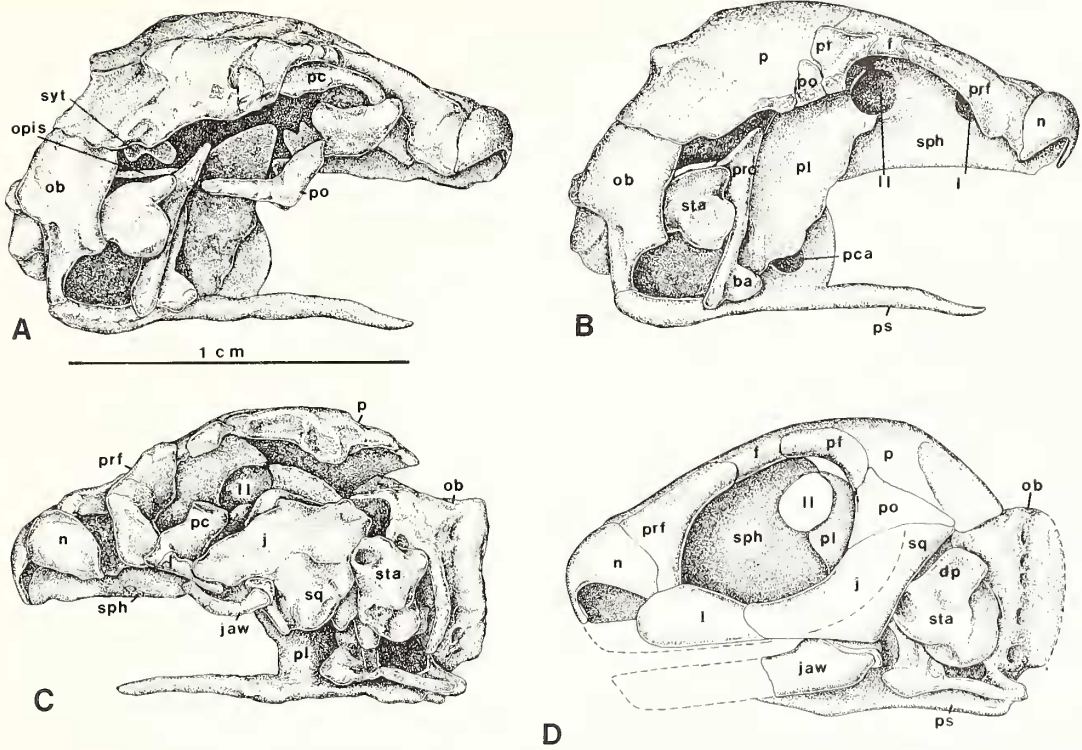
TEXT-FIG. 5. *Quasicaecilia texana*. A, right side of skull. B, restoration of the skull in right lateral view, with cheek removed to show braincase. C, left side of skull. D, restoration of skull in left lateral view; configuration of cheek is very speculative. Left and right sides have been independently restored. ×4·5.

the condition is reversed. The left capsule is somewhat compressed from back to front. Posteriorly, the opisthotics and exoccipitals are continuous with the supraoccipital, which extends forward a short distance beneath the overlying parietals.

The stapes is present in association with the fenestra ovalis on both sides, but on neither side is it in natural articulation. On the left side, the foot plate of the stapes is in continuity with the margin of the prootic in a clearly unnatural position that suggests minor dissolution and redeposition of the calcium phosphate during preservation. Otherwise the bone appears to retain its natural configuration. The foot plate extends for slightly less than 3 mm in dorsoventral diameter. It is not possible to reconstruct its exact position in the fenestra, but there may have been a medial unossified gap, as in several microsaurs (Carroll and Gaskill 1978). The stem of the stapes is somewhat less than 2 mm in diameter and 4 mm in length including the base of the foot plate. The stem appears to point anteroventrally, and ends in a shallow depression that may have been continued in cartilage. No stapedial foramen is evident. From the stem extends a broad but thin dorsal process that is almost parallel with the surface of the foot plate. What appears to be the right stapes is a simple columnar structure. It is about the size of the stem of the left stapes. Damage prior to burial may have led to the loss of the dorsal process and the margins of the foot plate.

Above the fenestra ovalis, the area of the inner ear continues to the skull roof. Medially, a further ossification is encountered that is not solidly fused to other elements. It is tentatively identified as an ossification of the synotic tectum. It bears grooves that may have accommodated the dorsal portion of the vertical semicircular canals. In several microsaurs (*Pelodosotis*, *Pantylus*, and *Rhynchonkos* [*Goniorhynchus*]), the supraoccipital continues anteriorly to incorporate the area of the synotic tectum, but this area appears to be separate in *Quasicaecelia*. In *Microbrachis*, in contrast, there is apparently no supraoccipital, but there is a more anterior ossification that may represent the synotic tectum. DeBeer (1937) recognized the presence of both a posterior tectum, which may ossify as the supraoccipital, and a more anterior synotic tectum in all major vertebrate

groups, but noted that their expression in individual species is extremely variable and appears to have little taxonomic significance.

In anterior view, the prootic appears as a nearly vertical sheet of bone that forms the anterior wall of the otic capsule. Ventrally, it is continuous with the parasphenoid-basisphenoid area. Just above the parasphenoid plate, a short area of unfinished bone is evident on both sides. It may have been in contact with the quadrate ramus of the pterygoid. Above this area the margin of the prootic is inflected posteriorly and somewhat medially into the fenestra ovalis.

Posteriorly, the prootic terminates some distance below the skull roof, along a line that corresponds to the dorsal margin of the fenestra ovalis. A very thin flange of bone, continuous with the surface of the right stapes, may represent the anterior extension of the opisthotic towards the prootic in this area. Anteriorly, the prootic extends further dorsally, narrowing to a point laterally. Anteromedially the prootic is notched for the prootic foramen, an opening formed jointly with the pleurosphenoid. The opening, clearly visible with minimal distortion on both sides, is approximately 0·9 mm in diameter, which is strikingly small relative to the other cranial dimensions.

At the base of the braincase, at the anterior margin of the posterior plate of the parasphenoid, are the basicranial processes which extend anteriorly as shelflike structures. No specific area of articulation is distinguished by unfinished bone surface. The adjacent margin of the pterygoid does not show a specialized area for the articulation between the braincase and the palate. Just anterior to the basicranial articulation are foramina that are comparable in position to those in caecilians which serve for the palatine arteries.

Anterior to the prootic, the area of the pleurosphenoid, most completely visible on the right side, forms the lateral wall of the braincase. It rises nearly vertically from the area of the basisphenoid-parasphenoid, and extends as a narrow sheet of bone to within less than 2 mm of the underside of the skull roof. It is lower posteriorly, where it is continuous with the prootic, and rises anteriorly. On the left side, it can be seen to form the posterior margin of a large opening for the optic and possibly the oculomotor nerves. The opening is about 2 mm in diameter, substantially larger than the opening for the Vth nerve. The pleurosphenoid forms the anterior margin of the oticoccipital portion of the braincase. Ventrally, there is a wide gap above the parasphenoid. Dorsally, the pleurosphenoid lies lateral of the sphenethmoid, apparently without being in sutural contract.

The anterior extent of the pleurosphenoid, beyond the level of the basicranial processes, would appear to preclude the origin of the rectus eye muscles from a retractor pit in the position of that structure in amniotes and anthracosaurian labyrinthodonts, as described by Clack and Holmes (1988). The high degree of specialization of all aspects of the braincase makes specific comparison with any labyrinthodonts difficult, however.

The posterior portion of the braincase is covered ventrally by the plate of the parasphenoid, indistinguishably fused to the overlying endoskeletal elements. The parasphenoid is marked on the left side by a strong ridge that formed the medial border of a groove for the carotid artery. This ridge is missing on the right side. The cultriform process of the parasphenoid extends forward like a dagger. It may have angled somewhat dorsally, but could not have underlain the sphenethmoid directly.

The sphenethmoid is visible in ventral and lateral views as a tubular structure extending anteriorly from the area of the pleurosphenoid to the front of the nasals. It appears to be closely appressed to the underside of the skull roof, beneath the frontals. Posteriorly, it forms the upper border of the foramen for the optic nerve, where it lies slightly medial to the pleurosphenoid. In contrast with caecilians, these bones do not abut against one another. Rather, the sphenethmoid appears to fit within the anterior borders of the pleurosphenoids.

The sphenethmoid is pierced laterally by relatively large foramina for the olfactory nerve. The anterior end of the bone is dorsoventrally compressed but widened laterally behind the front of the skull. This portion of the bone presumably served primarily as a structural brace since the foramina for nerve I exit more posteriorly, rather than at the end of the bone. The ventral border of the sphenethmoid is broadly rounded, but ends well above the cultriform process of the parasphenoid. In this it differs from other microsaurs in which the sphenethmoid is ossified, where it appears to be supported by the parasphenoid ventrally. The sphenethmoid is very incompletely ossified in early amniotes, but in genera in which it is preserved, there is also a wide gap between it and the cultriform process of the parasphenoid. The remainder of the braincase in this genus and early amniotes is so different that this one similarity is not thought to be taxonomically significant.

On the left side, just anterior to the otic capsule, is the posterior end of the lower jaw. The articular bone is in articulation with the condyle of the quadrate. Anteriorly it extends dorsally against the surface of the quadrate. Medially, the articular extends well beyond the remainder of the jaw. There is no retroarticular process. The anterior, tooth-bearing portion of the lower jaw is not preserved.

With no evidence of the postcranial skeleton, there is little basis for establishing the general adaptation of
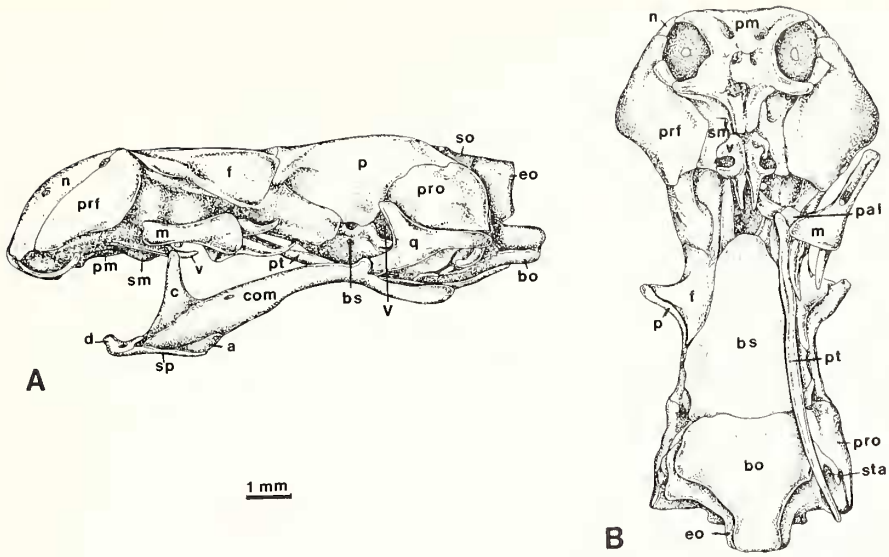
TEXT-FIG. 6. A, B, skull of the burrowing snake *Typhlops punctatus* in lateral and ventral views, modified from Parker (1977); small size of prootic foramen may be associated with reduction in size of jaws and dentition.

this species. A somewhat analogous modification of the cranial anatomy can be seen in burrowing typhlopid snakes (Text-fig. 6) in which the marginal jaw elements have lost their tooth-bearing role, and are much modified. As in caecilians, the fusion of the otic-occipital elements of the braincase might be attributed to a burrowing habitus, but such fusion did not occur in primitive burrowing snakes.

DISCUSSION

Taxonomic position

Despite the loss of their articulating surfaces, the great width of the exoccipitals and basioccipital in *Quasicaecilia* indicates the presence of wide condyles as in typical microsaurs. The pattern of the bones of the skull table resembles that of members of the Microbrachomorpha in the great width of the parietals and the progressively smaller size of the frontals and nasals. The greatest resemblance is to the previously described members of the family Brachystelechidae (Carroll and Gaskill 1987; Langston and Olson 1986) (Text-fig. 7). In both *Brachystelechus* and *Carrolla*, the
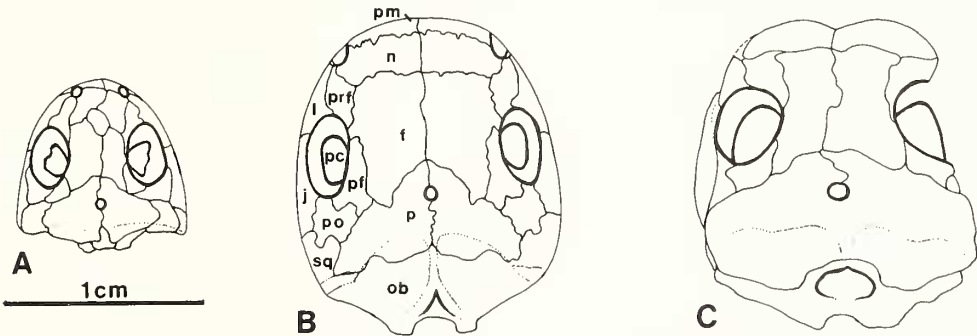
TEXT-FIG. 7. Skulls of the three genera assigned to the Brachystelechidae. A, *Brachystelechus*. B, *Carrolla*. C, *Quasicaecilia*.

parietals overlap the occipital surface, and the tabulars are either greatly reduced or entirely missing. All three genera have very wide skulls and possess palpebral cups.

Quasicaecilia resembles *Carrolla* in the high degree of ossification of the braincase; the cranial endoskeleton is not known in *Brachystelechus*. *Quasicaecilia* definitely differs from *Brachystelechus* in the shortness of the nasals, and from *Carrolla* by the absence of sutural attachment between the nasals and the premaxillae. *Quasicaecilia* also differs from *Carrolla* by the absence of a stapedial foramen and the separation of the sphenethmoid and the cultriform process of the parasphenoid.

The degree of specialization of these three genera appears to correspond with their stratigraphic succession. The relative age of specimens from the European Rotliegend succession is subject to continuing dispute, but Boy (1987) suggested that the horizon from which *Brachystelechus* was collected is roughly equivalent to the North American Admiral Formation. *Carrolla* comes from the Belle Plains Formation. *Quasicaecilia* is said to come from the Arroyo Formation, but this is indicated with a question mark on the label. No other described group of Palaeozoic tetrapods shares more derived characters in common with *Quasicaecilia* than do the previously identified members of the Brachystelechidae.

Affinities between goniorhynchid microsaurs and caecilians have been postulated on the basis of derived features of the braincase, several of which are also exhibited by *Quasicaecilia* (Carroll and Currie 1975; Walsh 1987; Jenkins and Walsh, in preparation). The fusion of the posterior portion of the braincase into a unitary os basale, the large size of the otic capsule, the presence of a large pleurosphenoid, the anterior position of the jaw articulation and the loss of dermal bones at the back of the skull table are features expected in the ancestors of caecilians (Walsh 1987). On the other hand, in all caecilians, premaxillae make up the anterior margin of the skull. Caecilians and their putative ancestors, the microsaur family Goniorhynchidae, are characterized by the small size of the orbits, in contrast with their large size in *Quasicaecilia*. Caecilians maintain the primitive pattern of having the sphenethmoid supported by the parasphenoid, in contrast with the derived condition seen in *Quasicaecilia*.

Many of the features in which *Quasicaecilia* resembles modern caecilians may be associated with small size and so do not constitute a strong basis for assuming close relationship.

Anatomical significance

The most interesting features of this specimen are the anatomical peculiarities, especially of the braincase. Among the most conspicuous are the great size of the otic capsule and stapes, but the relative size of the orbits and the configuration of the nasal region are also unusual.

The relatively large size of the sensory structures can be attributed primarily to the absolutely small size of the skull. The great importance of the sensory structures and the braincase in constraining the proportions of other features of the skull in small tetrapods was discussed in a compelling fashion by Hanken (1983, 1984) in his study of miniaturization in salamanders of the genus *Thorius*.

Although some species of modern frogs, salamanders, and caecilians are even smaller than this specimen, it is among the smallest Palaeozoic amphibians. Comparative dimensions of the braincase and sense organs of *Quasicaecilia* and other small tetrapods are given in Table 1.

In *Quasicaecilia* and other Palaeozoic tetrapods, the dimensions of the bony otic capsule and braincase can be measured directly. It is assumed that, as in other small tetrapods, the circumference of the eyeball closely matches that of the bony orbital margin. This is confirmed in many small Palaeozoic amphibians by the extent of the sclerotic ring which fills most of the orbital space. The size of the nasal capsule is more difficult to estimate. It is never ossified in Palaeozoic tetrapods (in contrast with their rhipidistian relatives). In some species, the extent of the capsule can be judged from impressions in the undersurface of the overlying dermal bones, but this area is only rarely exposed. In animals with small skulls, the probable size of the nasal capsule can be roughly estimated by the space available between the front margin of the skull and the anterior limit of the orbit, taking into consideration the position of the internal and external narial openings. In *Quasicaecilia*, the area of the nasal capsules appears to be outlined by the nasal bones that curve over the front

TABLE 1. Cranial dimensions of Palaeozoic and modern tetrapods. Area of sensory capsules and braincase are expressed as a percentage of the total skull area following the model of Hanken (1983). Measurements of *Thorius* and *Pseudoeurycea* from Hanken (1983). Measurements of *Ambystoma* from specimens in Redpath Museum. Measurements of fossils from literature cited in text.

Species	Skull length (mm)	Olfactory capsule (%)	Optic capsule (%)	Otic capsule (%)	Braincase (%)
Quasicaecilia texana	15	11	13	20	18
Cardiocephalus sternbergi	16	5	4	14	14
Brachydectes elongatus	18	7	9	19	23
Rhynchonkos stovalli	18	8	9	13	18
Doleserpeton annectens	11	8	25	9	18
Tersomius texensis	58	5	16	5	13
Phlegethontia longissima	23	6	15	12	20
Thorius pennatulus	3·3	14	27	17	37
Pseudoeurycea goebeli	10·6	17	18	11	23
Ambystoma jeffersonianum	15	9	11	11	22
Ambystoma tigrinum	19	14	12	11	15

margin of the skull, inclosing a circular space lateral to the opening for the olfactory tract. The extent of the nasal capsule is the most difficult of the sensory organs to estimate, but judging from modern salamanders, it is probably the least important in controlling the proportions of the skull.

Fortunately, the measures of the relative area of the entire skull and the sensory capsules used by Hanken can be compared directly with small Palaeozoic amphibians. The adult salamander specimens he measured range from 3·3 mm (*Thorius pennatulus*) to 10·6 mm (*Pseudoeurycea goebeli*) in skull length – all smaller than *Quasicaecilia*. Study of living forms shows that there is slight positive allometry shown by the nasal capsules, but strong negative allometry for the relative size of the otic capsule, eye, and braincase. These allometric relationships apply to both ontogeny within a particular species and to comparison between adults of different size within related groups.

The relative size of the nasal capsules, eyes, and braincase of *Quasicaecilia* are similar to those of salamanders measuring 15 and 19 mm in skull length, but are much smaller than those of the specimens examined by Hanken. In contrast, the otic capsules of *Quasicaecilia* are substantially larger than those of even the smallest salamander measured by Hanken, and approximately twice the size of those in salamanders in which the skull length is comparable to that of *Quasicaecilia*. In fact, nearly all the Palaeozoic specimens that were examined have very large otic capsules. The relatively large size of the semi-circular canals in Palaeozoic vertebrates has been discussed previously (Bernacsek and Carroll 1981). Several hypotheses have been advanced, but the specific physiological reason(s) for larger inner ear structures in early vertebrates has not yet been established. Presumably, early Palaeozoic tetrapods inherited this condition from their immediate ancestors among the rhipidistian fish. Although the data remain limited, it appears likely that the size of the otic capsule is an even more important factor in controlling the configuration of the skull in Palaeozoic tetrapods than it is in modern genera.

The otic capsules in *Quasicaecilia* dominate the back of the skull and extend to the margin of the cheek. As a result of their large size, the jaw suspension occupies a more anterior position and the adductor chamber is very small. This pattern is closely reminiscent of the early developmental stages of modern amphibians (DeBeer 1937). Ossification presumably occurred in an individual retaining essentially embryonic cranial proportions. The small size of the prootic foramen indicates a small Vth nerve, and reduced importance of the adductor jaw musculature. This, however, cannot be explained as a direct result of small skull size, since modern caecilians have skulls of even smaller size, and yet retain a large foramen for the Vth nerve.

The relatively anterior position of the orbits may also be attributed to the large size of the otic

capsules. In contrast, the configuration of the nasal bones and the absence of articulating surfaces for the premaxillae probably cannot be attributed simply to small size since the nasals are relatively long in the related genus *Brachystelechus*, which has an even shorter skull (estimated length 8·4 mm). *Carrolla*, a member of the same family, is approximately 15 mm long and has short nasals, but suturally attached premaxillary bones. The separation of the cultriform process from the sphenethmoid cannot be directly attributed to small size either, since the bones are in their normal position in *Carrolla*.

Examination of other genera (Text-figs 8 and 9) suggests that constraints related to the sense
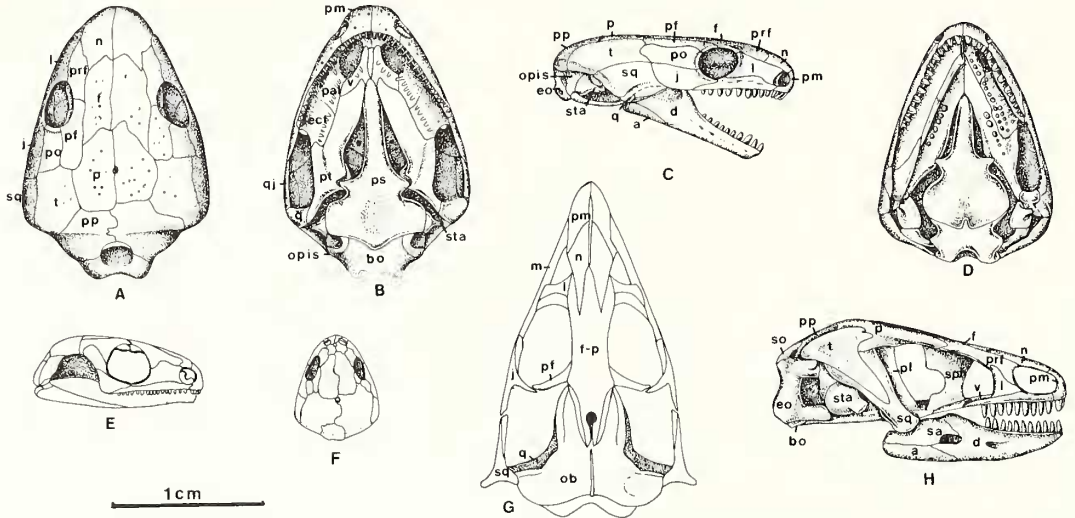

TEXT-FIG. 8. Skulls of amphibians less than 3 cm in length, all of which have large otic capsules and show modification in the position of the jaw articulation, adductor chamber and/or bones of the skull table. All ×2. A–F, microsaurs; A, B, *Rhynchonkos* [*Goniorhynchus*], in dorsal and palatal views; C, D, *Cardiocephalus sternbergi*, lateral and palatal views; E, *Hapsidopareion*, in lateral view. F, *Odonterpeton*, in dorsal view. G, the aistopod *Phlegethontia*. H, lateral view of the lysorophid *Brachydectes elongatus*. (A–F, from Carroll and Gaskill 1978; G, from McGinnis 1967; H, from Wellstead 1985.)
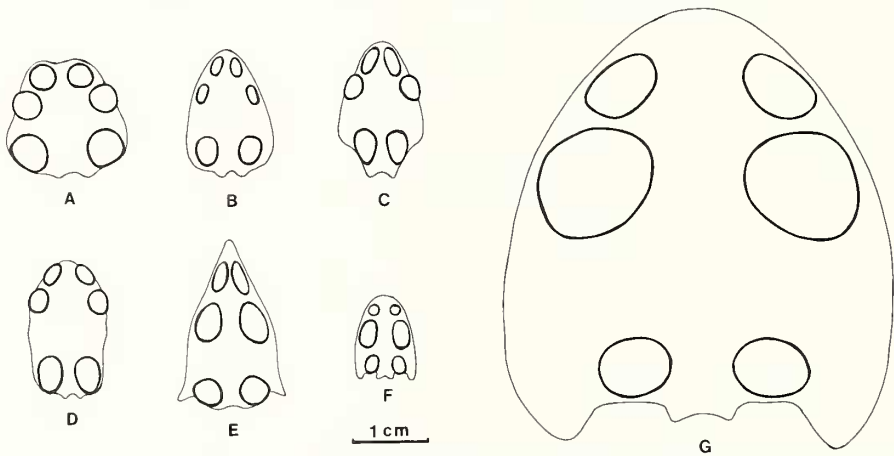
TEXT-FIG 9. Outline drawings of the skulls of small Palaeozoic tetrapods showing the areas of the sensory capsules. Drawn to a common scale. A, *Quasicaecilia*. B, *Cardiocephalus sternbergi*. C, *Rhynchonkos*. D, *Brachydectes elongatus*. E, *Phlegethontia*. F, *Doleserpeton*. G, *Tersomius*; in this genus the extent of the nasal and otic capsules have been established by serial sectioning.

organs may have a more general significance in determining the cranial anatomy of small animals belonging to a variety of Palaeozoic groups. The size of the orbits is extremely variable in Palaeozoic tetrapods, and the dimensions of the nasal capsules are difficult to estimate, but the otic capsule appears to retain a nearly constant size in small adults (Text-fig. 8) – from 13% to 20% of skull area in skulls less than 2 cm in length. Since the capsules extend nearly to the lateral margin of the skull, the area of the jaw articulation and/or adductor chamber is typically much modified.
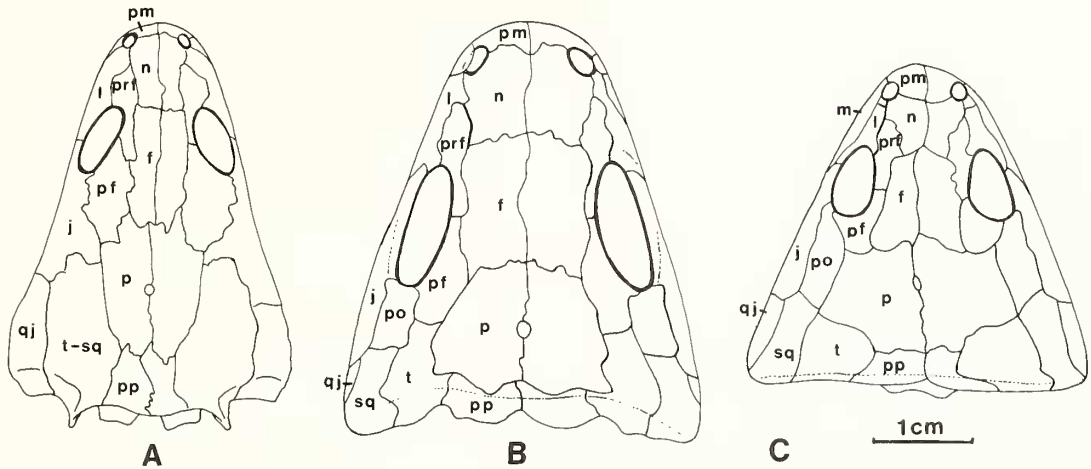
TEXT-FIG. 10. Skull roof of A, *Adelogyrinus*; B, *Asaphestera*; C, *Microbrachis*. Drawn to the same scale. The skulls of these genera are all greater than 3 cm long, and none shows evidence of modification resulting from a large otic capsule.

In the earliest and/or most primitive known members of the Adelogyrinidae and the two Microsauria suborders, Tuditanomorpha and Microbrachomorpha, the skull is still three centimeters or more in length (Text-fig. 10). The otic capsules are not known in these forms, but they would not be expected to be of sufficiently large size to require accommodation in the area of the jaw articulation or adductor chamber. In contrast, this has occurred separately within several microsaur families, and in the Lysorophia, Nectridea, and Aistopoda.

Members of the tuditanomorph microsaur families Goniorhynchidae, Hapsidopareiontidae, and Gymnarthridae, and the microbrachomorph *Odonterpeton triangularis* have skulls less than three centimeters in length. In the Goniorhynchidae and small gymnarthrids, the jaw articulation is anterior to the otic capsule. The jaw articulation remains in a posterior position in the Hapsidopareiontidae, but in some members of this family the cheek region is emarginated, enabling the jaw musculature to expand beyond the confines of the restricted adductor chamber. These three families retain the primitive pattern of the bones of the skull table. In contrast, they are much modified in *Odonterpeton*, in which the skull of the only known specimen is 6·7 mm in length. In this genus, the parietals are greatly expanded and the posparietals are reduced to a tiny median element.

However, there are apparent exceptions to the association between small skull size and modification of the otic region in two microsaur genera. Within the Hapsidopareiontidae, *Saxonerpeton* is known from several skulls, none more than 1·5 cm in length, but the jaw suspension and cheek region do not appear modified from the pattern of larger microsaurs. Although all the specimens of *Saxonerpeton* are moderately well ossified, they may not be of adult size. Several species of gymnarthrid microsaurs are known from the Lower Permian. They show a progressive shift in the position of the jaw articulation with decreasing skull size. In *Euryodus*, with a skull approximately 3·5 cm in length, the jaw articulation is posterior in position: essentially in the plane of the occiput. In *Cardiocephalus sternbergi*, the skull is approximately 1·6 cm in length, and the jaw articulation has shifted forward, 30% of the skull length (Carroll and Gaskill 1978, fig. 105). On

the other hand, a well-preserved skull of *Sparodus*, from the Upper Pennsylvanian, with a skull 3·3 cm long (Carroll 1988) also has the jaw articulation far forward. This may be attributed to a change in jaw mechanics associated with the large size of the marginal and palatal dentition, rather than to small size.

Among other lepospondyls, all members of the Lysorophia possess relatively small skulls, dominated by sensory structures. The jaw articulation is anterior to the otic capsule and the adductor chamber is open laterally (Wellstead 1985).

The configuration of the skull of aistopods (McGinnis 1967; Thomson and Bossy 1970; Wellstead 1982) is highly modified. All have an open cheek, although the jaw articulation retains a relatively posterior position in large individuals. In none of the described species is the adult skull less than 2 cm long, but the bones of the braincase are fused to one another and the otic capsules are large in *Phlegethontia*.
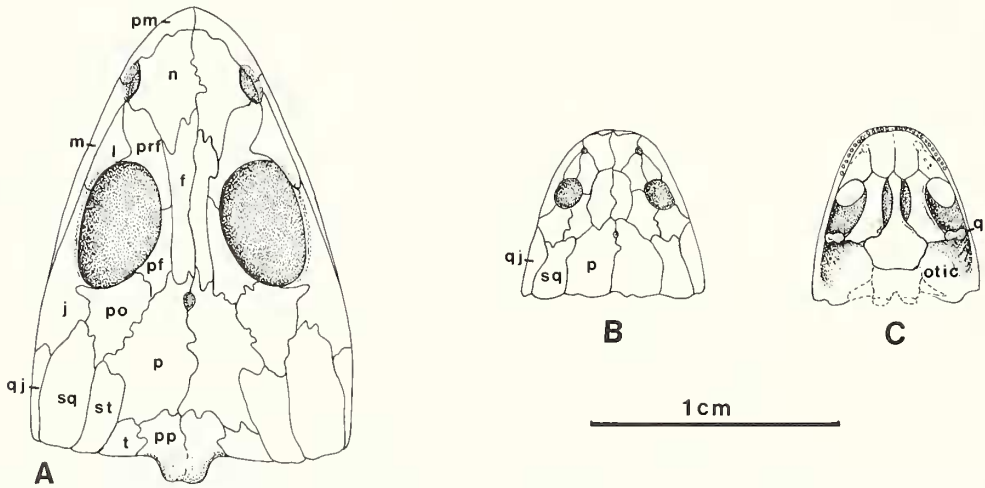
TEXT-FIG. 11. Nectridean skulls. A, *Ptyonius marshii* (from Bossy 1976). B, C, skull roof and palate of *Scincosaurus crassus* (from Milner 1978). Drawn to the same scale.

Ptyonius marshii (Text-fig. 11) is an early nectridean that has a skull shape resembling that of primitive labyrinthodonts except for the loss of the squamosal embayment, and retains all the primitive roofing bones except the intertemporal. The largest known skull is only 19 mm long. In contrast with some other nectrideans, the carpals and tarsals are not ossified, which suggests that even the largest specimens may not have reached maturity. *Scincosaurus crassus*, from the Upper Carboniferous of Czechoslovakia, has the smallest skull among possibly mature nectrideans – approximately 7 mm in length. What is known of the otic capsule indicates very large relative size, and the jaw articulation is displaced anteriorly. Postcranial remains are known of a related species from North America, but they indicate an animal only twice the size of the European form (Milner 1980).

As in modern salamanders (Hanken 1984), the relatively small size of all animals termed lepospondyls may contribute to the loss of dermal bones from the pattern seen in early labyrinthodonts. The fact that different bones are absent in microsaurs, nectrideans, and adelogyrinids suggests that they were lost independently in different lineages, each of which separately reduced their body size. If all animals termed lepospondyls evolved from a single common ancestor that had already reduced its skull size significantly, one would expect to observe a common pattern of bone reduction.

A general problem in interpreting the significance of small size among Palaeozoic tetrapods is the near impossibility of knowing whether the available specimens are of adult size. Frogs and

salamanders, whose egg size is constrained to less than 10 mm in diameter by the absence of extra-embryonic membranes (Carroll 1970), may increase their cranial dimensions many fold before reaching adulthood. This was presumably the case for Palaeozoic amphibians as well (Boy 1987). Since all amphibians are small at hatching, it is presumably the adult size that imposes the primary constraint on the dimensions of the sensory capsules. Only measurements of adults are hence of significance in evaluating the quantitative effects of small size. Unfortunately, there is no objective way of establishing whether an individual specimen is an adult. Broadly speaking, large tetrapods show progressive ossification as they approach adulthood, but species with very small adult size may become heavily ossified at a much earlier growth stage (Hanken 1982). Hence, extensive ossification of the ends of the limb bones and the braincase may be evidence that the specimen in hand represents a species that reaches maturity at small size, but not necessarily that this particular specimen is of adult dimensions.

None of the genera recognized as labyrinthodonts shows modification of the skull adjacent to the otic region that can be attributed to small size. Many tiny individuals have been described (Boy 1987) but all appear to be larvae or later immature stages. Bolt (1969, 1977) proposed that the dissorophoid labyrinthodont *Doleserpeton* might be close to the ancestry of the modern 'lissamphibian' orders. Milner (1988) argued that small size was an important factor in the origin of frogs, salamanders, and caecilians. The skull of *Doleserpeton*, although little more than 1 cm in length, retains the proportions of larger dissorophoid amphibians, and the otic capsule occupies no more than about 9% of its area, much less than that of *Quasicaecilia* and other small 'lepospondyls'.

Bolt (1979) has suggested that the material of *Doleserpeton* from Fort Sill might represent juvenile individuals of a genus resembling *Tersomius*, which reached a skull length of approximately 6 cm. The apparently small area of the otic capsule supports this interpretation. Even if *Doleserpeton* does belong to an assemblage that is the sister group of frogs and possibly salamanders, most of the osteological features that are characteristic of the modern orders must have evolved subsequently, presumably in relationship to significant reduction in adult skull size.

REFERENCES

BERNACSEK, G. M. and CARROLL, R. L. 1981. Semicircular canal size in fossil fishes and amphibians. *Canadian Journal of Earth Sciences*, **18**, 150–156.
BOLT, J. R. 1969. Lissamphibian origins: possible protolissamphibian from the Lower Permian of Oklahoma. *Science*, **166**, 888–891.
—— 1977. Dissorophoid relationships and ontogeny, and the origin of the Lissamphibia. *Journal of Paleontology*, **48**, 434–458.
—— 1979. *Amphibamus grandiceps* as a juvenile dissorophid: evidence and implications. 529–563. *In* NITECKI, M. H. (ed.). *Mazon Creek fossils*. Academic Press, New York, 581 pp.
BOSSY, K. V. H. 1976. Morphology, paleoecology and evolutionary relationships of the Pennsylvanian urocordylid nectrideans (Subclass Lepospondyli, Class Amphibia). Unpublished Ph.D. thesis, Yale University.
BOY, J. A. 1987. Studien über die Branchiosauridae (Amphibia: Temnospondyli; Ober-Karbon-Unter-Perm). 2. Systematische Ubersicht. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, Stuttgart*, **174**, 75–104.

CARROLL, R. L. 1970. Quantitative aspects of the amphibian–reptilian transition. *Forma et Functio*, **3**, 165–178.

—— 1977. Patterns of amphibian evolution: an extended example of the incompleteness of the fossil record. 405–437. *In* HALLAM, H. (ed.). *Patterns of evolution*. Elsevier, Amsterdam, 591 pp.

—— 1987. *Vertebrate paleontology and evolution*. W. H. Freeman and Company, New York, xiv + 698 pp.

—— 1988. An articulated gymnarthrid microsaur (Amphibia) from the Upper Carboniferous of Czechoslovakia. *Acta Zoologica Cracoviensia*, **31**, 441–450.

—— and CURRIE, P. 1975. Microsaurs as possible apodan ancestors. *Zoological Journal of the Linnean Society*, **57**, 229–247.

—— and GASKILL, P. 1978. The Order Microsauria. *Memoirs of the American Philosophical Society*, **126**, 1–211.

—— and HOLMES, R. 1980. The skull and jaw musculature as guides to the ancestry of salamanders. *Zoological Journal of the Linnean Society*, **68**, 1–40.

CLACK, J. A. and HOLMES, R. 1988. The braincase of the anthracosaur *Archeria crassidisca* with comments on the interrelationships of primitive tetrapods. *Palaeontology*, **31**, 85–107.

DAWSON, J. W. 1863. Air-breathers of the Coal Period. *American Journal of Science*, **36**, 430–432.

DEBEER, G. R. 1937. *The development of the vertebrate skull*. Oxford University Press, Oxford, 552 pp.

GAFFNEY, E. S. 1979. Tetrapod monophyly: a phylogenetic analysis. *Bulletin of the Carnegie Museum of Natural History*, **13**, 92–105.

GARDINER, B. G. 1983. Gnathostome vertebrae and the classification of the Amphibia. *Zoological Journal of the Linnean Society*, **79**, 1–59.

GAUTHIER, J. A., KLUGE, A. G. and ROWE, T. 1988. The early evolution of the Amniota. 103–155. *In* BENTON, M. J. (ed.). The phylogeny and classification of the tetrapods. *The Systematics Association Special Volume*, **35A**. Clarendon Press, Oxford, x + 377 pp.

HANKEN, J. 1982. Appendicular skeletal morphology in minute salamanders, genus *Thorius* (Amphibia: Plethodontidae): Growth regulation, adult size determination, and natural variation. *Journal of Morphology*, **174**, 57–77.

—— 1983. Miniaturization and its effects on cranial morphology in plethodontid salamanders, genus *Thorius* (Amphibia, Plethodontidae): II. The fate of the brain and sense organs and their role in skull morphogenesis and evolution. *Journal of Morphology*, **177**, 255–268.

—— 1984. Miniaturization and its effect on cranial morphology in plethodontid salamanders, genus *Thorius* (Amphibia: Plethodontidae). I. Osteological variation. *Biological Journal of the Linnean Society*, **23**, 55–75.

LANGSTON, W., JR. and OLSON, E. C. 1986. *Carrolla craddocki*, a new genus and species of microsaur from the Lower Permian of Texas. *Texas Memorial Museum Pearce-Sellards Series*, **43**, 1–20.

LINNAEUS, C. 1758. *Systema naturae*. (10th edn). L. Salvii, Stockholm, 823 pp.

MCGINNIS, H. J. 1967. The osteology of *Phlegethontia*, a Carboniferous and Permian aistopod amphibian. *University of California Publications in Geological Sciences*, **71**, 1–49.

MILNER, A. C. 1978. Carboniferous Keraterpetontidae and Scincosauridae (Nectridea: Amphibia) – a review. Unpublished Ph.D. thesis, University of Newcastle upon Tyne.

—— 1980. A review of the Nectridea (Amphibia). 377–405. *In* PANCHEN, A. L. (ed.). Environment and the origin of land vertebrates. *The Systematics Association Special Volume*, **15**. Clarendon Press, Oxford, xii + 633 pp.

MILNER, A. R. 1988. The relationships and origin of living amphibians. 59–102. *In* BENTON, M. J. (ed.). The phylogeny and classification of the tetrapods. *The Systematics Association Special Volume*, **35A**. Clarendon Press, Oxford, x + 377 pp.

—— SMITHSON, T. R., MILNER, A. C., COATES, M. L. and ROLFE, W. D. I. 1986. The search for early tetrapods. *Modern Geology*, **10**, 1–28.

PANCHEN, A. L and SMITHSON, T. R. 1987. Character diagnosis, fossils and the origin of tetrapods. *Biological Reviews*, **62**, 341–438.

—— —— 1988. The relationships of the earliest tetrapods. 1–33. *In* BENTON, M. J. (ed.). The phylogeny and classification of the tetrapods. *The Systematics Association Special Volume*, **35A**. Clarendon Press, Oxford, x + 377 pp.

PARKER, H. W. 1977. *Snakes: a natural history*. 2nd edition, revised and enlarged by A. G. C. Grandison. British Museum (Natural History) and Cornell University Press, Ithaca and London, 108 pp. + 16 plates.

RIEPPEL, O. 1988. A review of the origin of snakes. *Evolutionary Biology*, **22**, 37–130.

ROMER, A. S. 1966. *Vertebrate Paleontology* (3rd edn). Chicago University Press, Chicago, vii + 468 pp.

THOMSON, K. T. and BOSSY, K. H. 1970. Adaptive trends and relationships in early Amphibia. *Forma et Functio*, **3**, 7–31.

WALSH, D. M. 1987. Systematics of the caecilians (Amphibia: Gymnophiona). Unpublished Ph.D. thesis, McGill University.

WELLSTEAD, C. F. 1982. A Lower Carboniferous aistopod amphibian from Scotland. *Palaeontology*, **25**, 193–208.

—— 1985. Taxonomic revision of the Permo-Carboniferous lepospondyl amphibian families Lysorophidae and Molgophidae. Unpublished Ph.D. thesis, McGill University.

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